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Soils act as sinks or sources of CH_4 depending on air-filled porosity in sclerophyllous ecosystems in semiarid central Chile

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ABSTRACT

Carbon dioxide (CO_2) and methane (CH_4) are greenhouse gases (GHG), which sustained increase in the atmosphere contribute to global warming and climate change. The GHG fluxes of soils are strongly controlled by water content, temperature, plant and microbial communities and soil management. The Chilean sclerophyllous ecosystem is a global biodiversity hotspot historically and increasingly threatened by human activity. The aim of this study was to compare soil CH_4 (and CO_2) fluxes, under prevailing aerobic (dry hot summer) versus presumed partial anaerobic (wet winter) conditions, across a disturbance gradient in sclerophyllous ecosystems of central semiarid Chile. The CO_2 fluxes were measured with an infrared gas analyzer (IRGA) while CH_4 fluxes by gas chromatography using closed soil chambers. Soils were sources of CO_2 ($\sim 3.35\ \mu mol\ CO_2\ m^{-2}\ s^{-1}$) drastically changing with vegetation and seasons. Soils were generally sinks of CH_4 in summer ($\sim -3.75\ nmol\ CH_4\ m^{-2}\ s^{-1}$) and sources in winter ($\sim +4.12\ nmol\ CH_4\ m^{-2}\ s^{-1}$), which was mainly explained by air filled porosity. Modelled values showed that soils of the severely-disturbed *A. caven* savannah was overall a CH_4 source ($0.86\ g\ CH_4\ m^{-2}\ year^{-1}$), while the strongly-disturbed thorn scrub ($-0.56\ g\ CH_4\ m^{-2}\ year^{-1}$) and the moderately-disturbed sclerophyllous forest ($-2.68\ g\ CH_4\ m^{-2}\ year^{-1}$) were sinks. Hence protecting sclerophyllous forests and restoring disturbed ecosystems may contribute to mitigate anthropogenic CH_4 emissions.

1. Introduction

Greenhouse gases (GHG) maintain the temperature in the Earth's atmosphere, since they have the capacity to absorb radiation and reemit it as heat and also as radiation that is absorbed by the land. Increases in GHG concentration, as a result of anthropogenic activities, are responsible for the current global warming (IPCC, 2013). This effect has been accentuated by human activity with increasing emissions mainly as carbon dioxide (CO_2) and methane (CH_4). Atmospheric CO_2 concentrations are approximately 408 ppm, while CH_4 near 1.86 ppm (NOAA, 2018), although, CH_4 is about 23 times more efficient in heat capture than CO_2 (Chapin et al., 2012; Lechat et al., 2016).

Soil respiration releases a large portion of carbon fixed by photosynthesis partially regulating net ecosystem productivity, and hence global and regional carbon cycles (Luo and Zhou, 2006). Soil CO_2 effluxes are strongly controlled by water content (Balogh et al., 2011; Moyano et al., 2012; Cueva et al., 2015) and temperature (Balogh et al., 2011; Lellei-Kovács et al., 2011; Cueva et al., 2015), increasing exponentially with soil temperature in the absence of soil moisture limitations (Lloyd and Taylor, 1994; Guidolotti et al., 2013). When water limited, the CO_2 efflux increases with soil water content steadily until a threshold is reached (e.g. 20%) to even out thereafter (Luo and Zhou, 2006; Guidolotti et al., 2013).

The soil CH_4 fluxes are the result of two microbial processes: methanogenesis (CH_4 microbial production) in anaerobic conditions, and methanotrophy (CH_4 microbial consumption) under aerobic conditions (Chan and Parkin, 2001b; Dutaur and Verchot, 2007; Serrano-Silva et al. 2014). Water-saturated systems (such as wetlands) are sources of CH_4, whereas unsaturated soils (such as uplands) are CH_4 sinks (Warner et al., 2017). Methanogenesis (CH_4 soil emission) is strictly driven by archaea in anaerobic conditions, whereas methanotrophy (CH_4 soil uptake) is regulated by methanotrophic and nitrifying bacteria under aerobic conditions (Savi et al., 2016). Soils can act as sources and sinks for CH_4, depending on their air/water conditions (Chan and Parkin, 2001a). When soil water content is low, the air-filled porosity is high and therefore CH_4 diffusivity increases, favoring methanotrophy and hence CH_4 consumption (Epron et al., 2016, Fest et al., 2015). Soil CH_4 consumption can therefore be controlled by soil bulk density (Del Grosso et al., 2000; Fest et al., 2015), soil volumetric water content (Fest et al., 2015; Epron et al., 2016) and gas diffusivity (as measured by air filled porosity or water filled pore space) (Del Grosso et al., 2000; Dutaur and Verchot, 2007; Dalal and Allen, 2008; Fest et al., 2015;

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Epron et al., 2016). In contrast, methanogenesis and hence soil CH_4 emissions may occur in anaerobic soil pockets as a result of high soil bulk density and high volumetric water content decreasing air filled porosity and gas diffusivity (Dutaur and Verchot, 2007). In spite of the above, soil CH_4 exchange and its spatial variability is not fully understood, probably associated to the spatial and temporal variation of methanotrophic and methanogenic microbial activity (Christiansen et al., 2016).

The sclerophyllous scrubs and forests are the most common vegetation in Central Chile, where a semiarid mediterranean climate with a dry warm summer and cold rainy winter occur. These ecosystems exhibit a great diversity of plants due to the climate transition and hilly terrain (Gajardo, 1994; Luebert and Pliscoff, 2006); which is probably enhanced by a long history of degradation by cultivation, cattle grazing, fire and firewood extraction (Armesto et al., 2007; Bown et al. 2014).

The aim of this study was to compare soil CH_4 fluxes across a vegetation disturbance gradient of sclerophyllous scrubs and forests of Central Chile during a hot dry summer versus a mild wet winter. Also we aimed to better understand the environmental drivers controlling CH_4 fluxes. We hypothesized that soils will act as CH_4 sinks during the hot dry summer; where aerobic conditions prevailed, while as CH_4 sources during the mild wet winter when anaerobic conditions may arise.

2. Material and methods

2.1. Study site

The study was carried out in the National Reserve 'Roblería del Cobre de Loncha' (34° 08′ S, 71°03′ W), located in the Coastal Range, approximately 80 km southwest of the city of Santiago in central Chile. The physiography of the National Reserve watershed (5870 ha) is formed by non-continuous peaks cut by deep ravines and valleys, which largely determined the location of historical human settlement (UNDP, 2011). Parent materials are typically granitic, granodioritic and volcanic rocks (ODEPA, 1968; SERNAGEOMIN, 1982). The climate is Mediterranean, dry and semi-arid, with a mean annual precipitation of 503 mm, water deficit of 956 mm and mean annual temperature of 14.9 °C. Summer droughts extend for 6–8 months typically from October to April (CONAF, 2008).

The natural flora of the site is dominated by the tree sclerophyllous species *Cryptocarya alba* (Mol.) Looser. (Lauraceae), *Quillaja saponaria* Mol. (Quillajaceae), *Lithraea caustica* (Mol.) Hook. et Arn. (Anacardiaceae) and *Peumus boldus* Mol. (Monimiaceae), the invasive small N-fixing tree legume *Acacia caven* (Mol.) Mol. (Fabaceae) and the shrub species *Colliguaja odorifera* Mol. (Euphorbiaceae) and *Retanilla trinervia* (Gillies et Hook.) Hook. et Arn. (Rhamnaceae). These tree and shrub species are typical of the sclerophyllous forest, thorn scrub and *A. caven* savanna of Central Chile (Gajardo, 1994; Luebert and Pliscoff, 2006; Armesto et al., 2007).

The studied site was located in a toe slope in a north-aspect position. Soils developed from colluvial materials that belong to the coarse-loamy, mixed, thermic Typic Xerochrepts family (Soil Survey Staff, 1999) and locally associated with the Quilamuta Series (CIREN, 1996). Soil textures varied from loamy clay in the more disturbed sites to loamy sand in the less disturbed sites. Nine 25 × 25 m plots (625 m^2) were distributed equally across three clearly distinct vegetation types, henceforth identified as A, B and C (Fig. 1, Table 1), in increasing order of disturbance. Perennial cover decreased and species composition drastically changed from A to C. Plots ranged in altitude between 300 and 800 m above the sea level. The A condition, the least disturbed among A, B and C; is a second growth-coppice dominated by the tree species *C. alba*, *Q. saponaria* and *L. caustica*, with a tree cover ~50–75% and a leaf area index (LAI) ~3.26 $m^2 \times m^{-2}$. The strongly disturbed thorn scrub (B) has a sparse tree cover of sclerophyllous species (< 15%), notably *Q. saponaria* (up to 16 m in height) but also *C. alba*, *L. caustica* and *A. caven*, with medium shrub cover (~50%) of primarily *C. odorifera* and the thorny *R. trinervia* of less than 4 m in height (LAI ~ 2.86 $m^2 \times m^{-2}$, both shrub and tree cover). The severely-disturbed *A. caven* savanna (C) is a xerophytic open woodland dominated by the invasive leguminous tree *A. caven* (LAI ~ 0.12 $m^2 \times m^{-2}$) with emerging infrequent sclerophyllous trees of *Q. saponaria*, *C. alba* and *L. caustica*, with a dense herbaceous annual cover composed primarily of European annual herbs and grasses (e.g., slender wild oat, *Avena barbata* Pott ex Link) that are typically associated with grazing pastures (Armesto et al., 2007).

2.2. Soil CO_2 and CH_4 fluxes

Soil CO_2 and CH_4 fluxes were measured in the nine selected plots, three from each vegetation cover i.e. A, B and C. In each plot, measurements were also segregated by species cover. In the moderately-disturbed A situation, measurements were taken under *C. alba*, *L. caustica* and *Q. saponaria*. In the strongly-disturbed B condition, measurements were taken under *Q. saponaria*, *R. trinervia* and *C. odorifera*. In the severely-disturbed C condition, measurements were taken under the N-fixing leguminous *A. caven*, under the pasture, and under *Q. saponaria*. Therefore there were 3 vegetation covers × 3 plots per vegetation cover × 3 species cover per plot × 3 replicates per species cover × 2 seasons, which yielded 182 measurements.

Measurements were performed on rainless days between 10 am and 5 pm on the following dates: January 10–20, 2017 (summer) and June 5–July 12, 2017 (winter). Ninety one soil collars made of polyvinyl chloride (100 mm inner diameter and 50 mm length) were inserted into the soil across vegetation and species covers in September 2016. Soil CO_2 efflux (R_s) was measured in all collars within each plot using a closed chamber (100 mm inner diameter, Model SRC-1, PP Systems, Amesbury, MA, USA) connected to an infrared gas analyzer (Model EGM-4, PP Systems, Amesbury, MA, USA). Soil temperature (T_s) was measured simultaneously to R_s to a depth of 10 cm using a digital thermometer (PDT550, UEi, USA). Soil samples were taken to a depth of 20 cm around each collar to determine the soil gravimetric water content (θ_g). The bulk density (ρ_b) was determined using the parafin-sealed clod method (Blake, 1965). The volumetric water content (θ_v) was calculated as:

$$\theta_v = \rho_b \times \theta_g \quad (1)$$

Volumetric water content was converted into absolute air-filled porosity (AFP, $m^3\ m^{-3}$) knowing the bulk soil density (ρ_b) and the density of the solid phase (ρ_s) with the equation (Epron et al., 2016):

$$AFP = (1-\rho_b/\rho_s)-\theta_v \quad (2)$$

Soil particle density (ρ_s) was determined using the pycnometer method (Flint and Flint, 2002). This method is based on the displacement of water by solid particles (Archimedes method). The displacement of water was determined at 20 °C, by using 50 ml standard pycnometer flasks, which were partially filled with de-aired distilled water and then completed with 10 g (oven-dry basis) of soil. The particle density was then calculated as the ratio between the mass of the soil and the displaced volume of water.

Measurements of soil CH_4 fluxes were taken immediately after measuring soil CO_2 fluxes in each collar. To estimate soil CH_4 fluxes (F_{CH4}) we used a closed chamber made out of polyvinyl chloride (100 mm inner diameter, 200 mm length, with a stopcock on top). Gas samples were extracted from the static chambers using a plastic syringe (25 ml) and injected into pre-evacuated 12 ml vials (Exetainers, Labco Ltd., UK). CH_4 concentrations were determined by gas chromatography at the Soils Laboratory of Universidad de Concepción, Chillán, Chile. Blanks of CH_4 concentration were taken from the atmosphere and from the empty chamber three times per day as controls.

In an initial trial to know the time the chamber should be closed before extracting the 25 ml air aliquot, the CH_4 concentration was

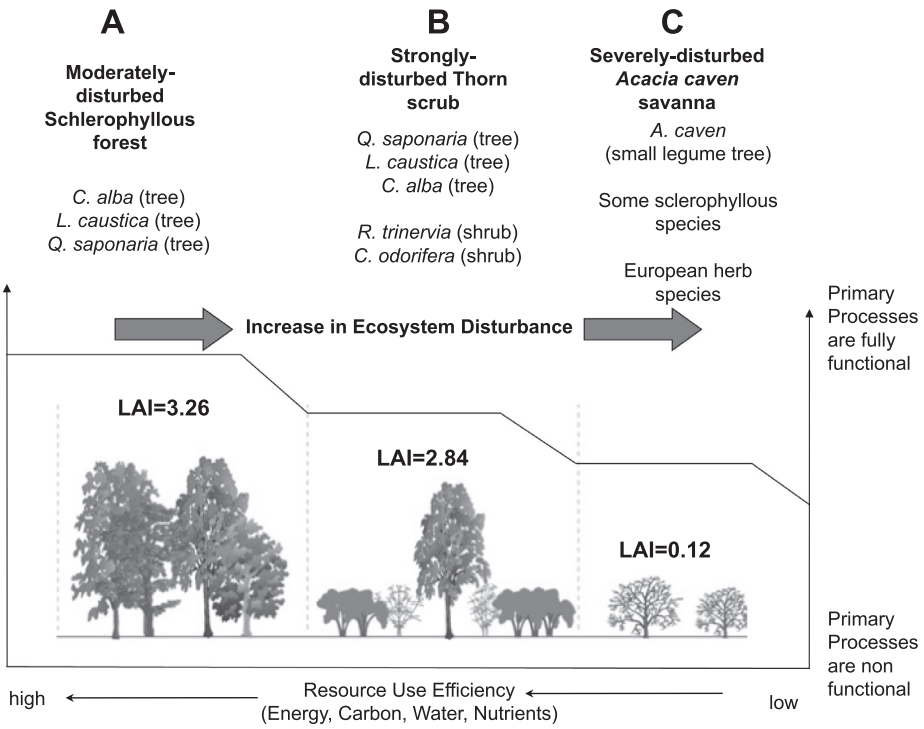

Fig. 1. Hypothetical model of the soil and vegetation disturbance of shrubland and sclerophyllous forests in Central Chile (based on Whisenant, 1999). The average leaf area index, LAI, ($m^2 m^{-2}$) is shown for each category.

followed over 40 min in the soil under two *Q. saponaria* trees in November 2016. The trend of the data indicated a decrease in the concentration of CH_4 inside the chamber over time (Fig. 2). It was considered that 10 min would be the minimum time at which a trend could be obtained. Therefore the soil CH_4 fluxes were estimated considering blanks of CH_4 concentration in open air, CH_4 concentrations at the end of 10 min in the closed soil chambers, and blanks of CH_4 concentrations at the end of 10 min in an empty chamber. Unsignificant differences in CH_4 concentrations were found between the blanks in open air and the closed empty chamber ($P < 0.001$).

Soil CH_4 fluxes were calculated with the following equation (Warner et al. 2017):

Table 1
Soil and vegetation variables across a disturbance gradient in the National Reserve Roblería del Cobre de Loncha in Central Chile.

Variable	Unit	Vegetation Type			ANOVA
		Moderately disturbed Sclerophyll. Forest (A)	Strongly disturbed Thorn Scrub (B)	Severely disturbed *Acacia caven* Savanna (C)	
Vegetation					
Basal Area	($m^2 ha^{-1}$)	23.8 ± 3.4 a	7.9 ± 2.7 ab	2.5 ± 0.7 b	**
Tree height	(m)	8.4 ± 0.5 a	7.6 ± 1.3 a	2.6 ± 0.6 b	**
Live crown height	(m)	4.2 ± 1.1 a	1.7 ± 0.3 ab	0.9 ± 0.2 b	**
Leaf Area Index	($m^2 m^{-2}$)	3.26 ± 0.75 a	2.84 ± 0.59 ab	0.12 ± 0.01 b	*
Shoots per hectare	–	2736 ± 226 a	619 ± 311 b	363 ± 77 b	**
Diam. at breast height	(cm)	9.5 ± 0.3	15.9 ± 4.9	8.7 ± 1.9	ns
Litter biomass	($g m^{-2}$)	71.3 ± 16.8 a	52.1 ± 8.8 ab	13.1 ± 2.6 b	*
Root biomass (0–30 cm)	($kg m^{-2}$)	4.69 ± 0.40 a	2.52 ± 0.34 b	2.36 ± 0.59 b	*
Soil					
Textural Class		Loamy sand	Loam	Loamy clay	
Sand		54.7 ± 3.0 a	44.8 ± 3.7 a	24.6 ± 5.6 b	***
Loam		32.0 ± 2.9	38.4 ± 3.9	37.6 ± 3.6	ns
Clay		13.4 ± 1.1 b	16.9 ± 1.6 b	37.8 ± 7.4 a	*
Bulk density	($g cm^{-3}$)	0.86 ± 0.23	1.2 ± 0.10	1.38 ± 0.16	ns
Particle density	($g cm^{-3}$)	2.35 ± 0.04	2.24 ± 0.07	2.25 ± 0.04	ns
Soil C	(%)	5.49 ± 0.89 a	2.92 ± 0.58 ab	2.03 ± 0.42 b	**
Soil N	(%)	0.41 ± 0.08	0.25 ± 0.08	0.21 ± 0.07	ns
Soil C/N	–	13.5 ± 0.6	12.4 ± 1.4	10.9 ± 1.6	ns

Soil and vegetation variables are presented as the means (± 1 SE, $n = 3$) for each vegetation type. The significance of the vegetation type is shown as the *P* range; ns: not significant; *: significant at $P \leq 0.05$; **: significant at $P \leq 0.01$; ***: significant at $P \leq 0.001$. Separation of the means was determined using a Tukey test. Different letters indicate significant differences at $P \leq 0.05$. The soil texture, bulk density, particle density, carbon and nitrogen concentrations were measured for the 0–10 cm soil depth. Soil and vegetation measurements were taken in 2010.

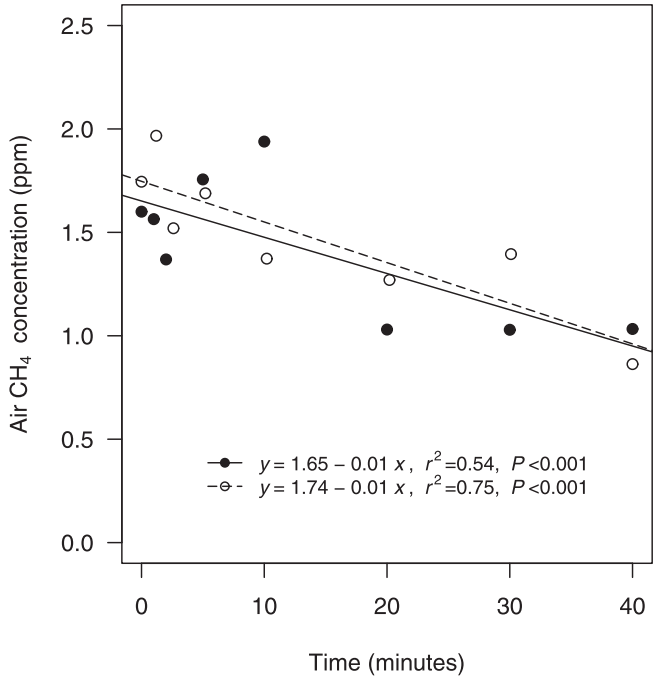

Fig. 2. Temporal change of CH_4 concentrations within a closed chamber system for two random measurements on soils under *Quillaja saponaria* taken in late spring of 2016 in a sclerophyllous ecosystem, central Chile.

$$F = \left(\frac{dC}{dt}\right)\left(\frac{V_c}{A_c}\right)\frac{R}{(R(T + 273.15))} \quad (3)$$

where F is the CH_4 flux, dC/dt is the change in CH_4 concentration per unit of time (nmol CH_4 mol^{-1} air s^{-1}), V_c is the closed system volume (0.00181 m^3), A_c is the chamber area (0.00825 m^2), P is the atmospheric pressure (101.325 kg m^{-1} s^{-2}), R is the ideal gas law constant (0.00831447 kg m^2 μmol^{-1} K^{-1} s^{-2}), T is the measured soil temperature (°C), and 273.15 is the conversion constant from Celsius to Kelvin.

The units usually used for the quantification of soil CO_2 emissions are $\mu mol\ m^{-2}\ s^{-1}$, while for CH_4 are $nmol\ m^{-2}\ s^{-1}$ (Warner et al., 2017). Positive values represent net emissions while negatives represent net uptake by soils.

2.3. Data analysis

All analyses were performed using R (R Development Core Team, 2014). Variables were tested for normality and homogeneity of variance, and transformations were made as necessary to meet the underlying statistical assumptions of the models used. A two-way analysis of variance (ANOVA) was used to test the main and interactive effects of vegetation type and season on R_s and F_{CH4}. Covariance analyses were performed to test whether the slopes and intercepts of the linear relationship between F_{CH4} and AFP significantly differed between vegetation types.

3. Results

3.1. Soil variables

The physical and chemical properties of soils (0–10 cm depth) differed drastically between vegetation types (Table 1). The severely-disturbed *A. caven* savanna (C) condition exhibited a greater proportion of clay (38%) and smaller proportion of sand (25%) than B (17%, 45%) and A (14%, 55%), while all conditions exhibited similar proportions of loam. Bulk density was the lowest (0.86 g cm^{-3}) and porosity the greatest (68%) in A compared to B (1.2 g cm^{-3}, 55%) and C (1.38 g cm^{-3}, 51%). Soil C (0–10 cm) was 5.49, 2.92 and 2.03% for A, B and C, respectively; while the soil C/N ratio did not differ between conditions being about 11–14 (Table 1).

3.2. Environmental variables

Air temperatures (and relative humidity) when sampling (10 am–5 pm) during summer ranged from 26 to 39 °C (13–33%) while 6 to 24 °C (24–76%) during winter. Soil temperature (and soil volumetric water content) ranged from 18.6 to 48.4 °C (1.2–8.4%) during summer and 5.3 to 18.1 °C (13–57%) during winter. Soil temperatures were higher, both in summer and winter, within the severely-disturbed open *A. caven* savannah (C; 35.1 °C, 12.4 °C) compared to the strongly-disturbed thorn scrub (B; 27.6 °C, 9.8 °C) and the moderately-disturbed sclerophyllous forest (A; 22.7 °C, 8.8 °C) (Table 2). In contrast, soil volumetric water content (θ_v) was only controlled by season ($P < 0.001$), being about 4% in summer and 23% in winter (Table 2). Air-filled porosity (AFP) was strongly influenced by vegetation, season and their interaction (Table 2), but overall, values were much greater in summer (average 39.1%) than in winter (average 20.1%), and also decreased from the moderately-disturbed sclerophyllous forest (A), to the strongly-disturbed thorn scrub (B) and the severely-disturbed open *A. caven*

Table 2
Changes in soil CO_2 and CH_4 fluxes, soil volumetric water content, soil temperature and air-filled porosity with vegetation (V) type and season (S).

Variable	Season	Vegetation type			ANOVA Statistics		
		A Moderately disturbed Sclerophyll. Forest	B Strongly disturbed Thorn Scrub	C Severely disturbed *Acacia caven* Savanna	S	V	S × V
CO_2 efflux	summer	2.93 ± 0.27^a	1.15 ± 0.12^b	1.38 ± 0.20^b	***	***	ns
($\mu mol\ m^{-2}\ s^{-1}$)	winter	6.95 ± 0.84^a	3.99 ± 0.51^b	3.42 ± 0.33^b			
CH_4 flux	summer	-4.93 ± 1.46^a	-4.18 ± 1.62^a	-2.16 ± 1.52^a	***	**	ns
($nmol\ m^{-2}\ s^{-1}$)	winter	0.08 ± 1.87^b	3.66 ± 1.17^{ab}	8.44 ± 1.90^a			
θ_v	summer	3.5 ± 0.4	3.5 ± 0.3	3.9 ± 0.3	***	ns	ns
(%)	winter	20.3 ± 1.3	24.9 ± 1.1	22.6 ± 1.1			
T_s	summer	22.7 ± 0.7^c	27.6 ± 0.8^b	35.1 ± 1.3^a	***	***	***
(°C)	winter	8.8 ± 0.3^b	9.8 ± 0.4^b	12.4 ± 0.6^a			
AFP	summer	44.6 ± 0.4^a	42.0 ± 0.3^a	30.8 ± 0.3^b	***	***	*
(%)	winter	27.8 ± 1.3^a	20.6 ± 1.1^b	12.1 ± 1.1^b			

Values are presented as the means (± 1 SE, n = 26–27) for each vegetation type. The significance of the vegetation type is shown as the P range; ns: not significant; *: significant at $P \leq 0.05$; **: significant at $P \leq 0.01$; ***: significant at $P \leq 0.001$. Separation of the means was determined using a Tukey test. Different letters indicate significant differences at $P \leq 0.05$. θ_v: soil volumetric water content; T_s: soil temperature at 10 cm; AFP: air-filled porosity (%).

savannah (C), although the decrease was steeper during winter than summer. Air-filled porosity (AFP) was related negatively with θ_v (Pearson-$r = -0.88$; $n = 162$; $P < 0.001$) across soil collars and plots.

3.3. Soil CO_2 and CH_4 fluxes

Soil CO_2 effluxes (R_s) were strongly controlled by season ($P < 0.001$) and vegetation type ($P < 0.001$) but not by their interaction ($P = 0.07$). The R_s values (mean ± 1 SE) were overall 2.6 times greater in winter (4.77 ± 0.38 μmol $m^{-2} s^{-1}$) than in summer (1.81 ± 0.15 μmol $m^{-2} s^{-1}$). Overall values of R_s were about two-fold greater in the moderately-disturbed (A) sclerophyllous forest (4.90 ± 0.51 μmol $m^{-2} s^{-1}$), compared to the strongly-disturbed (B) thorn scrub (2.54 ± 0.32 μmol $m^{-2} s^{-1}$) and the severely-disturbed (C) open *A. caven* savannah (2.40 ± 0.24 μmol $m^{-2} s^{-1}$) (Table 2).

Soil CH_4 fluxes were strongly controlled by season ($P < 0.001$) and vegetation type ($P = 0.004$) but not by their interaction ($P = 0.24$) (Table 2). In summer, soil CH_4 fluxes (mean ± 1 SE) were negative (−3.75 ± 0.88 nmol $m^{-2} s^{-1}$) i.e. soils consumed atmospheric CH_4, whereas in winter they were positive (4.12 ± 1.04 nmol $m^{-2} s^{-1}$) i.e. soils were sources of CH_4. Besides, there were marked differences among vegetation types. In summer, all soils were sinks of CH_4, but the moderately-disturbed (A) sclerophyllous forest exhibited a greater capacity to consume CH_4 (−4.93 nmol $m^{-2} s^{-1}$) compared to the strongly-disturbed (B) thorn scrub (−4.18 nmol $m^{-2} s^{-1}$) and the severely-disturbed open *A. caven* savannah (C) (−2.16 nmol $m^{-2} s^{-1}$) (Table 2). In winter, all soils were sources of CH_4, but the moderately-disturbed (A) sclerophyllous forest emitted drastically less CH_4 (0.08 nmol $m^{-2} s^{-1}$) compared to the strongly-disturbed (B) thorn scrub (3.66 nmol $m^{-2} s^{-1}$) and the severely-disturbed open *A. caven* savannah (C) (8.44 nmol $m^{-2} s^{-1}$) (Table 2).

When vegetation types (i.e. A, B, C) were segregated by tree and shrub species cover (i.e. *C. alba*, *L. caustica*, *Q. saponaria*, *C. odorifera*, *R. trinervia*, *A. caven*, Pasture), which approximately follows the compositional change with degradation, some interesting patterns for both soil CO_2 and CH_4 fluxes emerged (Fig. 3). Soil CO_2 effluxes were much greater in winter than summer, approximately decreasing in the order of compositional change with degradation i.e. *C. alba*, *L. caustica*, *Q. saponaria*, *C. odorifera*, *R. trinervia*, *A. caven*, Pasture. Soil CH_4 fluxes were negative in summer consuming CH_4 independent of species cover (Fig. 3), but during winter generally acted as sources of CH_4 (except for *C. alba*) and followed approximately the opposite pattern to soil CO_2 fluxes, generally increasing in the order of compositional change with degradation i.e. *C. alba*, *L. caustica*, *Q. saponaria*, *C. odorifera*, *R. trinervia*, *A. caven*, Pasture (Fig. 3).

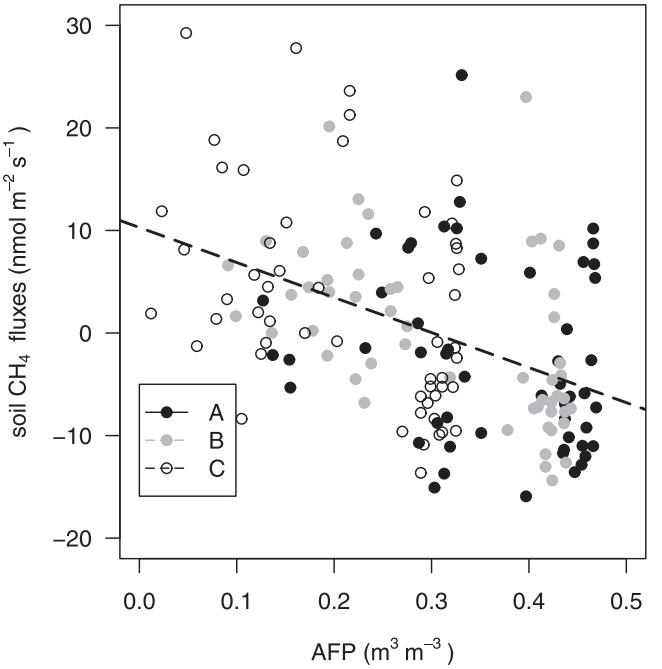

Fig. 4. Soil CH_4 fluxes as explained by air-filled porosity (AFP) and vegetation type (i.e. moderately-disturbed (A) sclerophyllous forest, strongly-disturbed (B) thorn scrub and severely-disturbed (C) open *A. caven* savannah).

3.4. Soil CO_2 and CH_4 fluxes and environmental variables

Soil CO_2 and CH_4 fluxes were positively correlated with soil volumetric water content (θ_v) (Pearson-$r = 0.49$ (CO_2), 0.38 (CH_4), $P < 0.001$), and negatively correlated with soil temperature (T_s) (Pearson-$r = -0.53$ (CO_2), −0.31 (CH_4), $P < 0.001$) and air-filled porosity (AFP) (Pearson-$r = -0.29$ (CO_2), −0.44 (CH_4), $P < 0.001$). Values of T_s, θ_v and AFP were strongly autocorrelated (Pearson-

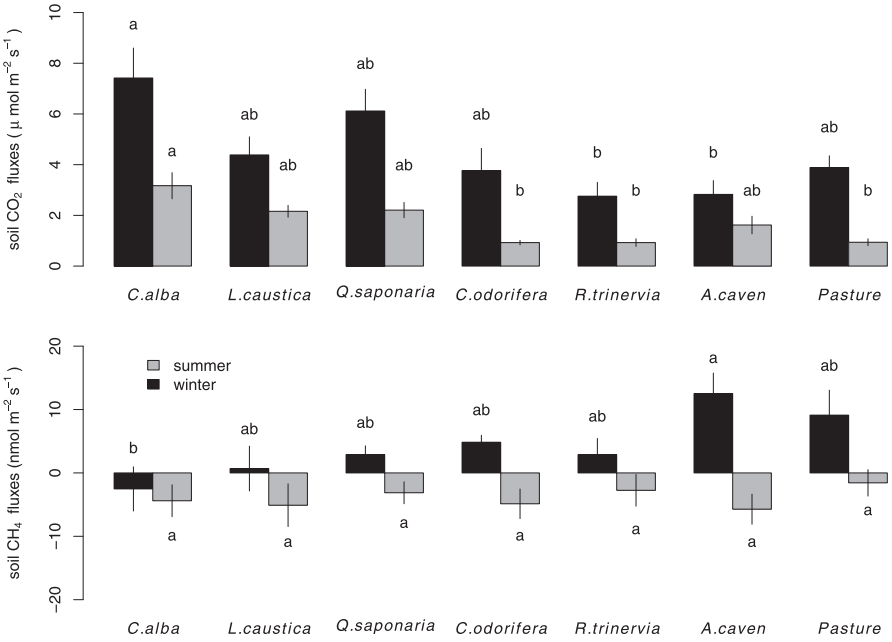

Fig. 3. Soil CO_2 and CH_4 fluxes along an approximate gradient in species compositional change with disturbance (i.e. *C. alba*, *L. caustica*, *Q. saponaria*, *C. odorifera*, *R. trinervia*, *A. caven*, Pasture). Values are presented as means ± 1 standard error with $n = 9$ for each species cover except for *Q. saponaria* where $n = 27$. Different lowercase letters indicate significant differences at $P < 0.05$ among species covers within seasons.

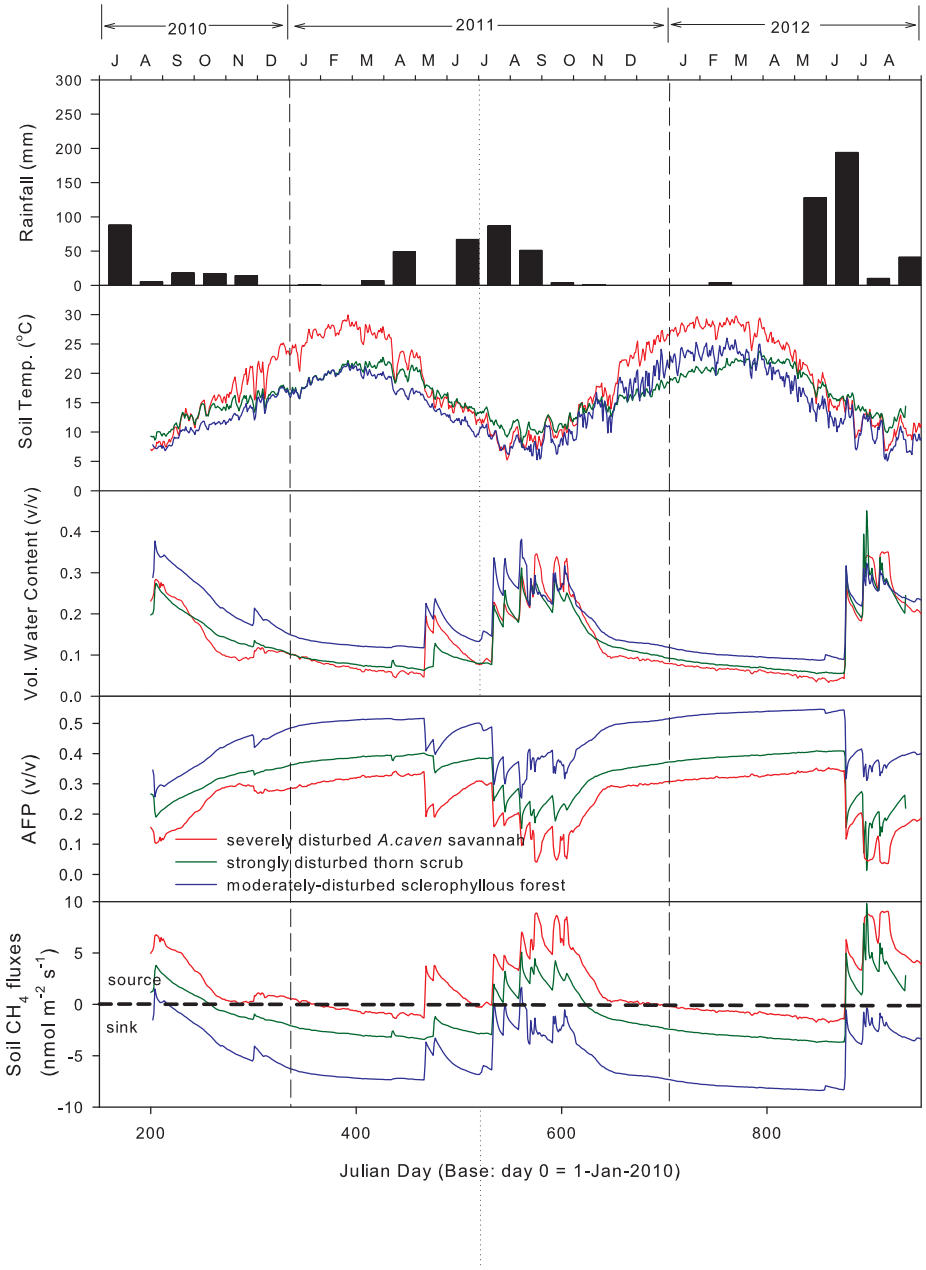
2010
2011
2012
J A S O N D J F M A M J J A S O N D J F M A M J J A
Rainfall (mm)
Soil Temp. (°C)
Vol. Water Content (v/v)
AFP (v/v)
severely disturbed A.caven savannah
strongly disturbed thorn scrub
moderately-disturbed sclerophyllous forest
Soil CH4 fluxes (nmol m-2 s-1)
source
sink
Julian Day (Base: day 0 = 1-Jan-2010)

Fig. 5. Rainfall, soil temperature, soil volumetric water content, air-filled porosity and modeled soil CH_4 fluxes across disturbance conditions for the period of July 2010–July 2012. Disturbance conditions are: A: moderately-disturbed sclerophyllous forest (blue line), B: strongly-disturbed thorn scrub (green line), and C: severely-disturbed *Acacia caven* savannah (red line). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

$r = -0.80$ for T_s vs θ_v; 0.54 for T_s vs AFP; -0.88 for AFP vs θ_v).

3.5. Soil CH_4 fluxes versus air filled porosity

Soil CH_4 fluxes (F_{CH4}) significantly decreased from positive (source) to negative (sink) as air-filled porosity (AFP) increased ($y = 10.29–34.16x$, $r^2 = 0.19$, $P < 0.001$; Fig. 4). Slopes ($P = 0.39$) and intercepts ($P = 0.92$) of this linear relationship were independent of vegetation type. The threshold value at which F_{CH4} equals zero from the equation above was 0.30, indicating that below an AFP of 30% anaerobic conditions may arise and hence soil CH_4 emissions may occur; while over 30% soil CH_4 consumption is likely to happen.

3.6. Modelled annual budget of soil CH_4 fluxes

Based on a previous dataset of daily soil volumetric water content for the years 2010, 2011 and 2012, for vegetation types A, B and C (Bown et al., 2014), values of soil bulk density and particle density (Table 1), we calculated AFP and modelled soil CH_4 fluxes on a daily basis, based on the equation showed in the precedent paragraph (i.e. $F_{CH4} = 10.29–34.16\ AFP$) (Fig. 5). We found that overall the soil of the severely-disturbed *A. caven* savannah acted as a CH_4 source ($0.86\ g\ CH_4\ m^{-2}\ year^{-1}$), compared to the other two conditions, the strongly-disturbed thorn scrub ($-0.56\ g\ CH_4\ m^{-2}\ year^{-1}$) and the moderately-disturbed sclerophyllous forest ($-2.68\ g\ CH_4\ m^{-2}\ year^{-1}$), which acted as CH_4 sinks.

4. Discussion

4.1. Soil CO_2 effluxes

Soil CO_2 effluxes measured in this study were similar to those reported by Rey et al. (2002) and Almagro et al. (2009) for Mediterranean zones but greater than those observed for other semiarid ecosystems (Rey et al., 2011). In our study, soil CO_2 effluxes drastically changed with season being much greater in the mild wet winter than in the hot dry summer. This seems contrary to the well documented exponential increase of soil respiration with temperature (Lloyd and Taylor, 1994) well linked to microbial metabolism (Rey et al., 2002, Warner et al., 2017). However smaller soil respiration rates in the hot dry season and greater in the wet season has also been shown in other studies in Mediterranean and semi-arid ecosystems (Almagro et al., 2009; Rey et al., 2002, 2011; Guidolotti et al., 2013). Soil respiration has been reported to increase with soil water content in arid and semi-arid ecosystems (Zhang et al. 2010), while declining severely in summer due to the effect of drought (Almagro et al., 2009). In our case, soil respiration was seemingly mainly driven by soil water content, although a strong autocorrelation between soil water content and soil temperature precluded us from adding soil temperature as a predictor of soil respiration.

The moderately-disturbed (A) sclerophyllous forest, the strongly disturbed (B) thorn scrub and the severely disturbed (C) open *A. caven* savannah were located in a toe slope of northern aspect so arguably compositional and structural vegetation changes can be attributed to disturbance by fire, wood extraction, cattle grazing and cultivation before the area was declared a National Reserve in 1996. Soil respiration decreased with disturbance in the series: A, B, C; similar to what has been found by Rey et al. (2011) in semiarid ecosystems across a disturbance gradient. We also segregated vegetation covers (i.e. A, B, C) into shrub and tree species covers (i.e. *C. alba*, *L. caustica*, *Q. saponaria*, *C. odorifera*, *R. trinervia*, *A. caven*, Pasture), which approximately follows the compositional change with degradation, finding that soil respiration generally decreased across this series (Fig. 3).

4.2. Soil CH_4 fluxes

Soil CH_4 consumption rates during summer in our study (A, 4.9; B, 4.2; C, 2.2; average 3.8 nmol $m^{-2} s^{-1}$) were on average 1.7 times greater compared to those reported by Warner et al. (2017) in a temperate forest in Maryland, USA, (2.2 nmol $m^{-2} s^{-1}$) while 2.4 times greater than those reported by Savi et al. (2016) in a Mediterranean holm oak (*Quercus ilex* L.) forest (1.6 nmol $m^{-2} s^{-1}$). Besides Savi et al. (2016) and Warner et al. (2017) mostly found CH_4 consumption but rarely emissions, while in our study soils were generally consumers in summer but sources in winter (A, 0.08; B, 3.66; C, 8.44; average 4.1 nmol $m^{-2} s^{-1}$) particularly for the most disturbed conditions (B, C). Our soil CH_4 emission rates (4.1 nmol $m^{-2} s^{-1}$) in winter, were 22–27 times smaller than those reported from temperate wetlands (i.e. 109 nmol $m^{-2} s^{-1}$, Cao et al. 1998; 91 nmol $m^{-2} s^{-1}$, Turetsky et al. 2014).

In semi-arid ecosystems, one of the most important environmental drivers of CH_4 fluxes is the soil water content (Dijkstra et al., 2013). Soils will act as net consumers when soil water content is low and aerobic conditions prevail while as producers of CH_4 when soil water content is high and anaerobic conditions may arise (Chan and Parkin, 2001b). We clearly observed this in our study with soils acting as consumers in summer and as sources in winter. Additionally we observed that soil CH_4 emissions, generally increased with disturbance (C > B > A) during winter; while soil CH_4 consumption followed the opposite pattern during summer (A > B > C). This suggests that soil CH_4 emission/consumption can also be controlled by management i.e. in our case well conserved or restored ecosystems will be stronger consumers and weaker sources of CH_4 than degraded ecosystems.

Soils are important consumers for CH_4 due to the action of methanotrophs in unsaturated soil conditions (Ueyama et al., 2015). These microorganisms oxidize CH_4 in aerobic environments (Luo and Zhou, 2006), which is why the negative fluxes (atmospheric CH_4 capture) detected in our study area correspond mainly to the summer season, where the soil presents aerobic conditions, since the pores are not saturated with water (average volumetric water content close to 4%). In contrast soils can act as sources of CH_4 under anaerobic conditions when water occupies the gaseous space of the soil (Fest et al., 2015), evidenced in our case through a high soil volumetric water content during the winter at about 24%.

4.3. Environmental controls on soil CH_4 fluxes

Anthropogenic disturbances, such as soil compaction, are generally considered to decrease the oxidation of CH_4 in the soil, since the properties related to the diffusion of gases are altered (Chan and Parkin, 2001b; Fest et al., 2015). We observed such a pattern, where the severely-disturbed (A) open *A. caven* savannah exhibited greater bulk density (1.38 g cm^{-3}), a smaller pore volume and likely greater anaerobism facilitating methanogenesis which translated more often in CH_4 emissions than in the moderately-disturbed (A) sclerophyllous forest (bulk density, 0.86 g cm^{-3}). On the other hand, less disturbed forests generally exhibit greater organic matter content, higher microbial activity, lower bulk density and greater porosity in the first layers of the soil profile than degraded ecosystems (Dutaur and Verchot, 2007). Also coarser textures facilitate greater gas diffusion and oxidation of CH_4 than finer textures (Dutaur and Verchot, 2007). In fact the severely-disturbed *A. caven* savannah exhibited a greater proportion of clay (38%) and a smaller proportion of sand (25%) compared to strongly-disturbed thorn scrub (17%, 45%) and the moderately-disturbed sclerophyllous forests (14%, 55%) (Table 1), which may explain why the severely-disturbed *A. caven* savannah emitted more CH_4 during the winter (Table 2). Once soil volumetric water content, bulk density and soil texture were accounted for in the calculation of air-filled porosity (AFP), soil CH_4 fluxes decreased with AFP independent of vegetation type (A, B, C), suggesting that in our study soil CH_4 fluxes were directly linked to conditions of aerobism and anaerobism. Epron et al. (2016) also showed the importance of AFP in explaining soil CH_4 fluxes in compacted soils.

4.4. Implications of the study

CONAMA (2006) predicts temperature increases of up to 4 °C and rainfall decrease of up to 40% in central Chile by the year 2100. Under this scenario, we may speculate that soil CH_4 consumption will increase because air-filled porosity would increase mediated by a reduction in soil water content. Considering that a better-conserved sclerophyllous ecosystem would act as a CH_4 sink (-2.68 g CH_4 m^{-2} $year^{-1}$), while a severely-disturbed open *A. caven* savannah as a source (0.86 g CH_4 m^{-2} $year^{-1}$), it follows that restoring degraded ecosystems may contribute towards ameliorating CH_4 anthropogenic emissions.

5. Conclusions

In conclusion, soil CO_2 and CH_4 fluxes were significantly influenced by season, and vegetation type. Soil CO_2 effluxes were greater in winter than summer which was mainly explained by soil water content. Soils generally consumed CH_4 during summer, when soils were dry and aerobic conditions prevailed; and sources of CH_4 during winter, when soils were wet and anaerobic conditions arise. Soil CO_2 effluxes drastically decreased with disturbance from the moderately-disturbed (A) sclerophyllous forest to the strongly-disturbed (B) thorn scrub and the severely disturbed (C) open *A. caven* savanah. Soil CH_4 emissions, on the other hand, generally increased with disturbance (C > B > A) during winter; while soil CH_4 consumption followed the opposite

pattern during summer (A > B > C). Modelled values showed that soils of the severely-disturbed *A. caven* savannah was overall a CH_4 source ($0.86\ g\ CH_4\ m^{-2}\ year^{-1}$), while the strongly-disturbed thorn scrub ($-0.56\ g\ CH_4\ m^{-2}\ year^{-1}$) and the moderately-disturbed sclerophyllous forest ($-2.68\ g\ CH_4\ m^{-2}\ year^{-1}$) acted as sinks, which may suggest that restoring degraded ecosystems may contribute towards ameliorating anthropogenic CH_4 emissions.

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